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Social constraint and an absence of sex-biased dispersal drive fine-scale genetic structure in white-winged choughs

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Abstract

This study used eight polymorphic microsatellite loci to examine the relative effects of social organization and dispersal on fine-scale genetic structure in an obligately cooperative breeding bird, the white-winged chough (*Corcorax melanorhamphos*). Using both individual-level and population-level analyses, it was found that the majority of chough groups consisted of close relatives and there was significant differentiation among groups (F_{ST} = 0.124). However, spatial autocorrelation analysis revealed strong spatial genetic structure among groups up to 2 km apart, indicating above average relatedness among neighbours. Multiple analyses showed a unique lack of sex-biased dispersal. As such, choughs may offer a model species for the study of the evolution of sex-biased dispersal in cooperatively breeding birds. These findings suggest that genetic structure in white-winged choughs reflects the interplay between social barriers to dispersal resulting in large family groups that can remain stable over long periods of times, and short dispersal distances which lead to above average relatedness among neighbouring groups.

Keywords: cooperative breeding, *Corcorax melanorhamphos*, dispersal, genetic structure, sex-bias, spatial autocorrelation

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Introduction

Dispersal behaviour plays a critical role at multiple scales in animal ecology yet because of the difficulties involved in the study of dispersal behaviour, our understanding of the causes and consequences of dispersal are limited (Slatkin 1985; Walters 2000). By necessity, field studies are restricted both temporally and spatially. Consequently, direct methods of estimating dispersal such as mark–recapture methods and radio tracking may fail to detect long-distance or infrequent dispersal and result in estimates that are heavily biased towards short-distance, regular dispersal events (Slatkin 1985; Koenig *et al*. 1996).

Using genetic estimates of dispersal can avoid some of the problems associated with obtaining accurate field data. Equilibrium-based statistics, such as Wright's *F*-statistics, measure the degree of genetic differentiation between populations and in some species have revealed unexpectedly high rates of gene flow between distant populations that could not have been detected using observational data alone (e.g. grey-crowned babblers, *Pomatostomus temporalis*, Edwards 1993; Australian magpies, *Gymnorhina tibicen*, Baker *et al*. 2001; *Naso vlamingii*, Klanten *et al*. 2007). *F*-statistics can also be used to investigate sex differences in dispersal behaviour (Goudet *et al*. 2002). However, these methods are based on assumptions that may be inappropriate for many species (Whitlock & McCauley 1999). In addition, *F*-statistic estimates will mostly reflect historical processes rather than current dispersal behaviour (Bossart & Prowell 1998). As a complement to *F*-statistics, the availability of hypervariable genetic markers such as microsatellites has made it possible to investigate contemporary patterns of dispersal and population structure at a microgeographical scale through the development of individual-based statistical techniques such as assignment indices and spatial autocorrelation analysis (Peakall *et al*. 2003; Paetkau *et al*. 2004; Double *et al*. 2005).

Restricted dispersal within populations is expected to result in positive local spatial genetic structure where relatedness between individuals declines with increasing geographical distance. Analyses that explicitly measure the relationship between genetic distance and geographical

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distance such as Mantel tests (Smouse *et al*. 1986) and spatial autocorrelation analysis (Epperson & Li 1996) have been widely used to detect genetic structure in plants (e.g. Epperson & Alvarez-Buylla 1997; Chung *et al*. 2000; Marquardt & Epperson 2004; Jones *et al*. 2007) but less so in animals. However, the combination of microsatellite markers and multivariate spatial autocorrelation methods such as the multilocus, multi-allele method of Smouse & Peakall (1999) have proved highly sensitive for detecting unexpected fine-scale genetic structure in animals. For example, Peakall *et al*. (2003) detected significant local positive structure in Australian bush rats (*Rattus fuscipes*) at a scale of less than 1 km. Similarly, Double *et al*. (2005) investigated microgeographical genetic structure in superb fairy-wrens (*Malurus cyaneus*) and found significant positive structure at a scale of less than 500 m. Spatial autocorrelation analysis has also been used to examine the effects of habitat fragmentation on the spatial genetic structure of geckos (*Oedura reticulata* and *Gehyra variegata*; Hoehn *et al*. 2007), beetles (*Adelium calosomoides* and *Apasis puncticeps*; Schmuki *et al*. 2006), agile antechinus (*Antechinus agilis*; Banks *et al*. 2005) and the common frog (*Rana temporaria*; Johansson *et al*. 2005).

In addition to restricted gene flow, local positive genetic structure may be generated by social behaviour where socially defined population structure at a local scale results in nonrandom mating and close spatial associations between relatives (Chesser 1991a, b; Sugg *et al*. 1996). In cooperative breeding birds, the social structure of the population is often characterized by natal philopatry and female-biased dispersal. In many species offspring delay dispersal, often forgoing independent reproduction, and remain on their natal territory to assist the reproductive efforts of their parents (Brown 1987). One of the potential benefits of remaining on the natal territory is the opportunity to gain breeding positions in neighbouring territories or even appropriate part of the natal territory for independent breeding (Ekman *et al*. 2004). Therefore, sex-biased dispersal in cooperative breeders is often coupled with short-distance dispersal by the philopatric sex (Zack 1990) resulting in close spatial associations between relatives. Consequently, fine-scale positive spatial genetic structure is expected in such species, particularly in the philopatric sex.

Few studies have examined the consequences of social behaviour on microgeographical genetic structure in cooperatively breeding birds. Painter *et al*. (2000) observed significant genetic structure in plural-breeding, cooperative bell miners (*Manorina melanophrys*) at three levels of social organization: 'nesting contingents', 'coteries' and 'breeding colonies'. Breeding colonies showed significant genetic differentiation, as did coteries within colonies that were separated by as little as 40 m. Coteries, which consisted of one or more nesting contingents, were comprised of closely related, philopatric males. However, there was no evidence of increased rates of inbreeding within each coterie due to strongly female-biased dispersal (Clarke & Heathcote 1990). Recent work on the population genetic structure of apostlebirds (*Struthidea cinerea*) also revealed high levels of relatedness within social groups and significant differentiation between social groups due to natal philopatry and short dispersal distances (Woxvold *et al*. 2006). In the first study to apply spatial autocorrelation to a cooperative breeding bird, Double *et al*. (2005) found that even with obligate female dispersal, male philopatry in superb fairy-wrens was sufficient to maintain positive genetic structure over the population as a whole but led to significant sex differences in the spatial distribution of genetic variation. Positive genetic structure was only observed in males, reflecting sex differences in dispersal behaviour. However, the behavioural mechanisms generating positive structure in male fairy wrens are complex and the competing processes of restricted male dispersal and high rates of extra-group paternity could not be fully disentangled. The study by Double *et al*. (2005) highlights the necessity of observational data to fully evaluate the likely behaviours generating positive genetic structure. Recently, Temple *et al*. (2006) have also used spatial autocorrelation analysis to confirm sex-biased dispersal in the endangered white-breasted thrasher (*Ramphocinclus brachyurus*).

Here we investigate the population genetic consequences of the interplay between social structure and dispersal in the obligately cooperatively breeding bird, the white-winged chough (*Corcorax melanorhamphos*). Previous ecological studies of choughs suggest that like their closest relatives the apostlebirds, dispersal is rare and extremely sporadic. Unlike many cooperatively breeding birds, offspring of both sexes remain with their natal group which may remain stable for more than 10 years and is generally thought to consist of a monogamous breeding pair and their offspring from multiple years (Rowley 1978; Heinsohn 1991a). However, the genetic relationships within and between social groups have not been investigated previously. We combine both individual-level and population-level genetic analyses to: (i) estimate relatedness within social groups; (ii) determine whether positive local spatial genetic structure occurs at the individual or group level; (iii) evaluate the genetic evidence for sex-biased dispersal; and (iv) evaluate the collective evidence for the relative contributions of restricted dispersal and social organization to the observed genetic patterns within chough populations.

Materials and methods

Study species

White-winged choughs are large, insectivorous, ground-foraging birds endemic to the eucalypt woodlands of southeastern Australia that live year round in groups ranging in size from 3 to 20 individuals (Rowley 1978).

Choughs are obligate cooperative breeders, pairs have never been observed to reproduce successfully and even trios rarely succeed in fledging young (Heinsohn 1992). Chough groups do not defend stable territories, but maintain overlapping home ranges of up to 1000 ha in size. Home ranges contract during the breeding season to an area of approximately 20 ha surrounding the nest site (Rowley 1965).

Field methods and study population

Between June 2002 and March 2005, we caught and banded almost 400 individuals from approximately 40 chough groups in and around Canberra in the Australian Capital Territory, Australia. Groups were caught using walk-in cage-traps baited with cheese. Once caught, birds were weighed, aged using iris colour (Rowley 1975) and banded with individually numbered leg bands. Choughs can be aged until birds reach 4 years of age as eye colour changes from dark brown in fledglings to red in adults. Age was classified as '1' (birds in their first year), '2' (birds in their second year), and so on up to 'adult' (4 years old and above). A small (~50 μL) blood sample was taken from the brachial vein and stored in 70% ethanol for use in genetic analyses. All methods were approved by the Australian National University Animal Experimentation Ethics Committee.

A census of group size and group composition was recorded approximately twice a week during the breeding season (August–March) and at least twice during the non-breeding season. For the purposes of the analysis that follows, we included all banded birds that were known to be alive at the beginning of the 2003 breeding season, defined as August 1, 2003. This sample included 201 birds in 37 groups. Groups were defined as those collections of individuals which were together on August 1 and subsequently attempted to breed. Group sizes ranged from 3 to 13 with a mean of 6.8 and modal group size of six. The proportion of group members sampled ranged from 50% to 100%. The sex ratio [M/(M + F)] of the total population was 0.47 (95 males and 106 females) and not significantly different from parity ($x_1^2 = 0.14$, $P = 0.7$), but within each group ranged from 0.2 to 0.8. The sex ratio within each age class ranged from 0.38 for birds in their second year, to 0.52 to birds in their first year (1 = 0.52; 2 = 0.38; 3 = 0.49; 4 = 0.42; adult = 0.49). The geographical distribution of study groups within the broader study area (based on nest sites) is shown in Fig. 1. Nearest neighbour distance (NND) ranged from 10 m, where two groups shared the same nest site, to approximately 4 km, with a mean of 665 m (± 980 m SD; Fig. 2).

Molecular analysis

DNA extraction. DNA was extracted from blood by ammonium acetate extraction (Richardson *et al*. 2001) after digestion with proteinase K (Progen), and resuspended in low EDTA TE buffer (10 mM Tris, 0.1 mM EDTA, pH 7.5–8.0).

Molecular sexing. White-winged choughs are monomorphic and sex cannot be determined from any visual or frequently observed behavioural cues (Rowley 1978). The sex of each individual was therefore determined using the molecular technique developed by Griffiths *et al*. (1998) which involves the amplification of a sex-linked CHD gene.

Microsatellite genotyping. All samples were genotyped at eight polymorphic microsatellite loci (Table 1) using the dye-labelled M13 primer genotyping method described by Schuelke (2000). Polymerase chain reaction amplifications were performed on an FTS–960 Thermal Sequencer (Corbett Research) using the reaction protocol and touch-down thermal cycling programme described in Beck *et al*. (2003). This programme was modified for two loci; CmeH2 and Sci1. For CmeH2, the final annealing temperature was increased from 50 °C to 52 °C. Amplification of Sci1 used the following programme: 2 min at 94 °C; 30 s at 94 °C, 30 s at 52 °C and 30 s at 72 °C for 35 cycles and a final extension step of 72 °C for 5 min. Loci were run on an ABI 3100 capillary electrophoresis system with an internal size standard and scored using GeneMapper 3.0 (Applied Biosystems).

Statistical analysis

Genetic variation, relatedness and population structure. Unless stated otherwise, all analyses were performed using GENALEX 6.1 (Peakall & Smouse 2006). Allele frequencies, observed and expected heterozygosities, and the fixation index were calculated for each locus. We tested deviations from Hardy–Weinberg equilibrium in GenePop 3.4 (Raymond & Rousset 1995) using the exact probability test. This test was performed on a random sample of 50 adult individuals to avoid any confounding effects of the known family structure. Markov chain parameters were set to 100 batches with 1000 iterations per batch.

Pairwise relatedness estimates of Lynch & Ritland (1999) *R* were calculated for each pair of individuals and mean pairwise relatedness calculated for each group. We estimated the 95% confidence interval around mean pairwise group *R* via bootstrapping. Random permutation of the data set was used to generate a distribution for the null hypothesis of no relatedness among individuals within groups and to provide a test for significance. All bootstrapping and permutational tests were performed 1000 times. We compared mean pairwise relatedness within each sex over the total population and mean within-group pairwise relatedness for each sex using GENSTAT for Windows, 8th Edition (Genstat Committee 2005). Only those groups that contained more than one member of each sex were included in the group analysis.

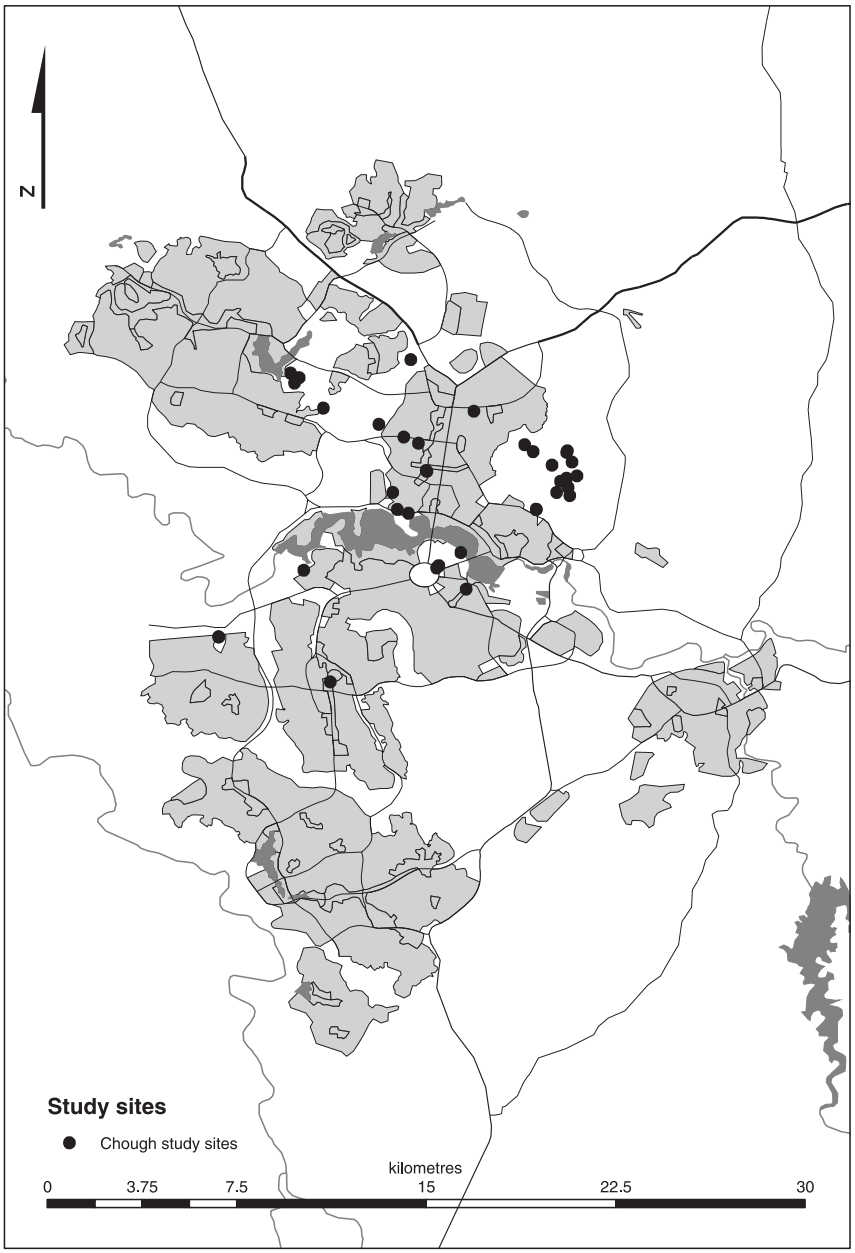

Fig. 1 Distribution of groups sampled in the Australian Capital Territory (ACT). Light grey areas represent urban areas. Lakes are shown in dark grey. Dots represent the nest sites of each group included in the study.

For the analysis of population structure, we used the social group as the unit of subdivision. An analysis of molecular variance (AMOVA) framework was used to estimate multilocus F_{ST} and the partitioning of genetic variation within and among social groups following the method of Excoffier *et al*. (1992), extended for use with codominant loci by Peakall *et al*. (1995). Statistical significance was tested by 1000 random permutations. We calculated group F_{ST} for each sex separately in order to detect evidence of sex-biased dispersal. Where dispersal is sex biased, F_{ST} for the more philopatric sex is expected to be higher than that of the dispersing sex (Goudet *et al*. 2002).

Spatial autocorrelation

Spatial autocorrelation analysis provides a measure of genetic correlation as a function of distance. The analysis of spatial autocorrelation was performed using the genetic-distance-based, multivariate approach developed by Smouse & Peakall (1999). This approach enables multiallele, multilocus analysis, thereby strengthening the spatial signal. This method requires as inputs a geographical and a genetic distance matrix. Pairwise genetic distance was calculated for codominant data following the method of Smouse & Peakall (1999). Geographical distance between

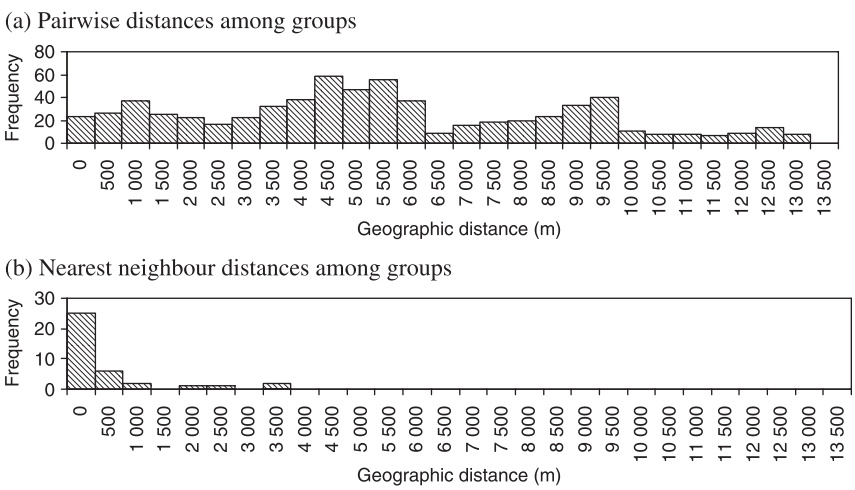

Fig. 2 Frequency distributions of (a) pairwise distances among groups and (b) nearest neighbour distances among groups.

Table 1 Microsatellite loci used in the analysis. Data refer to results from 201 individuals

Locus	Repeat motif	M13 primer	Allele number	Size range	H_O	H_E	F	P
CmeA1	$(CTTT)_{44}(ATCT)_9$	NED	20	224–346	0.88	0.93	0.059	< 0.001
CmeC1	$(CTTT)_3(CTAT)_{14}$	FAM	10	162–202	0.69	0.66	–0.042	
CmeG5	$(TATC)_{10}(CCAT)_7$	NED	6	177–193	0.72	0.71	–0.015	
CmeH2	$(CT)_{25}$	VIC	9	145–167	0.85	0.84	0.000	
CmeH9	$(GT)_{17}$	VIC	7	209–225	0.84	0.83	–0.010	
LEI160	$(VG)_{12}(AG)_{13}$	FAM	4	179–187	0.64	0.60	–0.056	
Pgm4	$(CTTT)_5$	VIC	14	275–327	0.81	0.87	0.060	< 0.001
Sci1	$(GAAA)_7AAA(GAAA)_{26}GA$ $(GAAA)_{22}(GA)_6(GAAAGAGA)_2$	FAM	43	168–350	0.92	0.96	0.040	< 0.001

H_O, observed heterozygosity; H_E, expected heterozygosity. References: CmeA1, CmeC1, CmeG5, CmeH2, CmeH9: Beck *et al*. (2003); LEI160: D. A. Dawson, R. Buckland, K. W. Fok, I. R. K. Stewart & T. Burke, Department of Animal and Plant Sciences, University of Sheffield (unpublished), Gibbs *et al*. (1997); Pgm4: Dowling *et al*. (2003); Sci1: Woxvold *et al*. (2006).

groups was calculated from global positioning system coordinates of the nest site of each group. This spatial autocorrelation analysis provides an estimate of the autocorrelation coefficient, *r*, for each group of individuals separated by a specified geographical distance. This coefficient is bounded by –1 and +1 and has a mean of zero where there is no autocorrelation (Smouse & Peakall 1999). The analysis produces a correlogram of spatial autocorrelation as a function of distance. Significance was tested by random permutation which provided an estimate of *r* and 95% confidence intervals about the null hypothesis of no spatial genetic structure ($r = 0$). If the correlogram fell outside the 95% confidence interval bounding the null hypothesis, significant spatial structure was indicated. The 95% confidence interval around *r* was estimated via bootstrapping as described in Peakall *et al*. (2003).

In order to compare the patterns of spatial genetic structure between males and females, we generated separate geographical and genetic distance matrices for males and females and applied the 'Multiple Pops' spatial option in GENALEX. This procedure enables the separate analysis of male, female and total with appropriate permutation procedures for the combined total analysis (see Peakall *et al*. 2003 for details). This same approach was taken for comparing the spatial genetic structure differences between subadults (< 4 years) and adults (≥ 4 years).

Despite its importance, a clear rationale for the choice of distance classes used in spatial autocorrelation analysis is frequently lacking in published spatial genetic analysis studies. Choice of distance class size can strongly influence the outcomes since the ability to detect spatial autocorrelation reflects the interplay between the distance class sizes chosen and the true but unknown extent of spatial genetic structure (Peakall *et al*. 2003). In the present study, given prior insight into the cooperative breeding strategy of choughs (Heinsohn 1991a), we predicted that the spatial genetic patterns will reflect two processes: (i) social structure (within group patterns of relatedness), and (ii) dispersal (the amount and extent of movement of individuals among groups). In this context, we paid careful attention to the appropriate choice of distance classes in order to enable us to tease out these two different processes.

To assist us in making an informed decision about distance classes, we generated frequency distributions of the nearest neighbour distances among groups, and the distribution of all pairwise distances among groups using routines in GENALEX (see Fig. 2). Inspection of these two frequency distributions enabled us to select distance class boundaries (based on consideration of the multimodal nature of the distributions) that reflected sensible biological classes. For example, we set our first distance class to zero to include all those comparisons within groups. Inspection of the frequency distribution of nearest neighbour distribution revealed that for most groups, the nearest neighbours nested within 500 m, hence the second distance class of greater than zero up to 500 m was selected to represent 'very near' neighbours. The next most frequent nearest neighbour distance was less than 1000 m, while the maximum distance between nearest neighbours was 3500 m. We defined these groups as 'near neighbours' and subdivided them into distance classes of 1000, 2500 and 3500 m for the purposes of analysis. The selection of distance class boundaries beyond the nearest neighbour distances (> 3500 m) was based on consideration of the frequency distribution of all pairwise distances, with the boundaries of distance classes chosen to encompass one of the multimodes of the distribution. For example, the distance class between > 6000 and 10 000 m encompassed the third mode of the frequency distribution. Note that there is no requirement for distance classes to be even in spatial autocorrelation analysis (Smouse & Peakall 1999).

Because our interest in this study was both at the individual and group level, we also performed spatial autocorrelation analysis at the group level. To achieve this, the average genetic distance among all pairwise combinations of the groups was computed as follows. For a given pair of groups, the individual-by-individual codominant genotypic distances were calculated (as for the individual analysis above) across all pairs of individuals representing the specific among group contrasts and the average calculated for this set, and so on for each pairwise combination of groups. The group genetic distance calculations were performed in a customized version of GENALEX. This option will be freely available in GENALEX 6.2. As an average, the magnitude of the among-group genetic distances is comparable to the individual-by-individual genetic distance, but allows spatial genetic analysis among populations with average among-group genetic distance matrices, and a matrix of geographical distance among groups as the inputs for spatial autocorrelation. For comparison with the individual-by-individual spatial analysis, we applied the same distance classes (other than the within-group class).

To further evaluate the spatial genetic patterns among groups, we applied the two-dimensional local spatial analysis method (2D LSA) described by Double *et al*. (2005) and available as an option in GENALEX (Peakall & Smouse 2006). This novel method provides a heuristic tool for investigating the local patterns of spatial genetic autocorrelation within the two-dimensional landscape. The method employs a sampling strategy that focuses on a subset of points surrounding a pivotal data point. For each subset, the extent of local autocorrelation is estimated according to the method of Smouse & Peakall (1999), based on the n pairwise comparisons between the pivotal data point and its n nearest neighbours. In the present study, our interest was to assess whether there was heterogeneity across the landscape in relation to the patterns of autocorrelation among the groups. Therefore, unlike Double *et al*. (2005) here we applied 2D LSA at the group, rather than the individual level using as inputs the same genetic and geographical matrices as used in the group level spatial analysis.

To complement the group level spatial analysis, we also performed Mantel tests of matrix correspondence as a test for isolation by distance with tests of significance by random permutation (following Peakall *et al*. 2003). Mantel tests for isolation by distance were performed using both geographical distance (GGD) and log(1 + GGD) matrices against both average among-group genetic distance and pairwise F_{ST} matrices.

Tests for sex-biased dispersal

To test for sex-biased dispersal, we used the corrected assignment index (AIc) developed by Favre *et al*. (1997) which applies a modification of the assignment test method of Paetkau *et al*. (1995). This test determines the expected frequency of each individual's genotype in the population from which it was sampled, corrected for population effects. AIc for each individual was calculated as the individual log-likelihood minus the mean log-likelihood of the population for total males and females and for adult (≥ 4 years) males and females separately. For each analysis, overall AIc values will average to zero for the population as a whole with a significant difference in the means of males and females if sex-biased dispersal occurs. Negative AIc values with larger variances are also expected for the dispersing sex (Mossman & Waser 1999).

Results

Genetic variation, relatedness and population structure

The number of alleles per locus, and observed and expected heterozygosities are shown in Table 1. Allele number ranged from 4 to 43 per locus and observed heterozygosity values ranged from 0.64 to 0.92. No locus showed a significant departure from Hardy–Weinberg equilibrium across the set of 50 randomly selected samples.

Within-group mean pairwise relatedness estimates were calculated only for those groups where at least 75% of the group had been sampled (n = 27) and ranged from

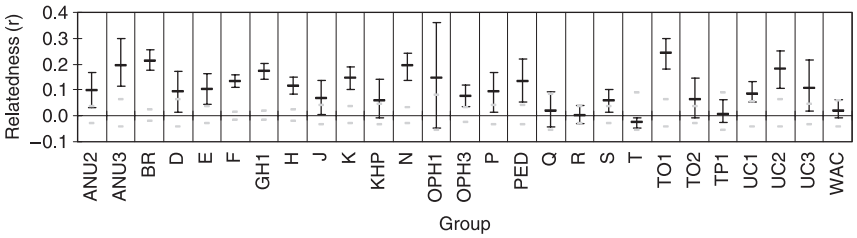

Fig. 3 Mean within-group pairwise relatedness estimates for 27 groups where more than 75% of the group members were sampled. Grey lines represent permuted 95% confidence intervals around the null hypothesis of zero relatedness and error bars represent bootstrapped confidence intervals around the mean.

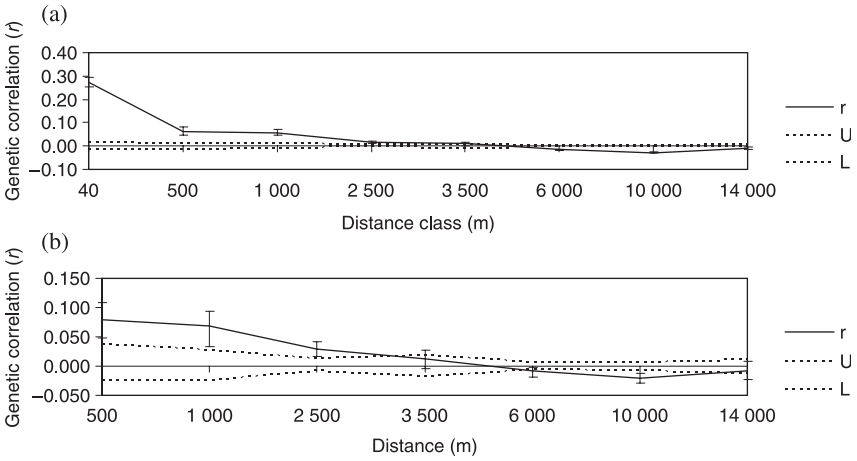

Fig. 4 Correlogram plots of the spatial genetic autocorrelation coefficient *r* as a function of distance for (a) individuals and (b) groups. Upper U and lower L bounds for the 95% confidence interval about the null hypothesis of no spatial structure ($r = 0$) and the upper U*r* and lower L*r* 95% error bars about *r* as determined by bootstrap resampling are shown.

–0.028–0.241 (Fig. 3). Mean pairwise relatedness within groups was significantly greater than zero in 70% (19/27) of groups (Fig. 3), and was positively correlated with group size (correlation = 0.38). Pairwise relatedness between same sex group members was calculated for those groups with two or more members of each sex ($n = 25$). Relatedness between females in the same group ranged from –0.056 to 0.280 with a mean of 0.125 ± 0.02 SE and was not significantly different to the mean within-group pairwise relatedness between males which ranged from –0.042 to 0.289 with a mean of 0.125 ± 0.02 SE (two-tailed *t*-test, $t_{44} = -0.01$, $P = 0.99$). Nor was there a significant difference between estimates of mean female relatedness ($R = -0.003 \pm 0.001$ SE) and mean male relatedness ($R = -0.003 \pm 0.001$ SE) across the entire study population (two-tailed *t*-test, $t_{10028} = -0.11$, $P = 0.92$).

Analysis of molecular variance revealed significant differentiation among groups ($F_{ST} = 0.124$). However, pairwise differentiation among groups varied considerably from 0.00 to 0.352. There was no significant differentiation between males ($F_{ST} = 0.123$) and females ($F_{ST} = 0.130$).

Spatial autocorrelation analysis

Spatial autocorrelation analysis revealed significant positive spatial genetic structure (Fig. 4a). The first distance class, representing within-group comparisons, showed significant positive spatial structure, similar to the estimates of average within-group relatedness. However, significant positive structure extended well beyond the within-group comparison, with the three distance classes that included near neighbours all exhibiting similar positive *r* values (Table 2), with x-intercepts in the range of 4500 m.

Spatial autocorrelation analyses run separately for males and females revealed very similar results among the sexes, with both sexes closely matching the outcomes for the total data set (Table 2). However, differences were detected among age classes, with subadults showing significantly stronger genetic structure than adults both within groups (0.333 versus 0.189, 95% CIs not overlapping), as well as among very near neighbour groups. However, for both subadults and adults significant positive genetic structure was detected up to the distance class of 3500 m (Table 2).

The group level spatial analysis also revealed significant local positive autocorrelation based on the average among group genetic distance. Proximate groups were, on average, more genetically similar than more distant groups (Fig. 4b). The outcomes of Mantel tests of matrix correspondence confirmed this pattern of isolation by distance revealing a significant positive relationship between average group genetic distance and geographical distance ($Rxy = 0.172$, $P = 0.035$). For the transformation log(1 + geographical distance), the relationship was stronger ($Rxy = 0.278$, $P = 0.001$). Equivalent tests of the relationship between pairwise group F_{ST} values and genetic distance revealed the same trends, but the magnitude of the correlations was not as strong ($Rxy = 0.012$, $P = 0.428$; for the log(1 + geographical distance) transformation, $Rxy = 0.134$, $P = 0.033$).

Table 2 Outcomes of spatial genetic autocorrelation analysis. Separate results are provided for all individuals, adults, subadults, females and males. The correlation *r* is shown across eight distance classes with zero representing within-group comparisons. The number of pairwise comparisons *n*, upper U and lower L bounds for the 95% confidence interval about the null hypothesis of no spatial structure ($r = 0$), the upper U*r* and lower L*r* 95% error bounds about *r* as determined by bootstrap resampling, the probability *P* of a one-tailed test for positive autocorrelation, and the estimated x-intercept are also shown

Distance class (end point m)	0	500	1000	2500	3500	6000	10 000	14 000	Intercept
Category	Within group	Very near	Near			Far		Very far	
All individuals									
n	518	651	804	2812	1229	6859	5281	1946	
r	0.274	0.064	0.058	0.015	0.009	–0.017	–0.028	–0.010	
U	0.014	0.013	0.010	0.005	0.008	0.003	0.003	0.005	
L	–0.014	–0.012	–0.011	–0.005	–0.009	–0.003	–0.003	–0.005	
U*r*	0.022	0.016	0.013	0.006	0.009	0.003	0.004	0.007	
L*r*	0.022	0.016	0.013	0.006	0.009	0.004	0.004	0.006	
P(*r-rand* ≥ *r-data*)	0.001	0.001	0.001	0.001	0.019	1.000	1.000	1.000	4362
Adults									
n	178	311	363	1258	372	2234	1685	502	
r	0.189	0.043	0.049	0.011	0.013	–0.016	–0.024	–0.008	
U	0.026	0.017	0.015	0.007	0.016	0.004	0.005	0.008	
L	–0.024	–0.015	–0.015	–0.007	–0.015	–0.006	–0.005	–0.011	
U*r*	0.037	0.023	0.021	0.009	0.017	0.006	0.007	0.012	
L*r*	0.039	0.021	0.020	0.009	0.015	0.007	0.006	0.012	
P(*r-rand* ≥ *r-data*)	0.001	0.001	0.001	0.002	0.047	1.000	1.000	0.940	4620
Subadults									
n	85	76	82	362	250	1173	971	404	
r	0.333	0.121	0.077	0.017	0.018	–0.017	–0.032	–0.009	
U	0.035	0.037	0.035	0.016	0.019	0.007	0.007	0.011	
L	–0.034	–0.033	–0.034	–0.012	–0.018	–0.008	–0.009	–0.012	
U*r*	0.056	0.056	0.039	0.016	0.021	0.009	0.009	0.014	
L*r*	0.052	0.052	0.035	0.015	0.021	0.008	0.009	0.014	
P(*r-rand* ≥ *r-data*)	0.001	0.001	0.001	0.020	0.031	0.999	1.000	0.925	4769
Female									
n	132	195	237	716	325	2005	1303	652	
r	0.310	0.068	0.055	0.011	0.013	–0.015	–0.029	–0.016	
U	0.030	0.022	0.019	0.011	0.018	0.005	0.007	0.008	
L	–0.029	–0.021	–0.018	–0.011	–0.017	–0.006	–0.007	–0.010	
U*r*	0.043	0.033	0.023	0.011	0.017	0.006	0.007	0.011	
L*r*	0.044	0.031	0.023	0.011	0.017	0.007	0.008	0.011	
P(*r-rand* ≥ *r-data*)	0.001	0.001	0.001	0.024	0.068	1.000	1.000	0.999	4649
Males									
n	106	140	168	689	282	1428	1337	315	
r	0.300	0.051	0.045	0.020	0.013	–0.013	–0.033	–0.002	
U	0.034	0.027	0.024	0.011	0.017	0.006	0.006	0.012	
L	–0.030	–0.024	–0.022	–0.011	–0.017	–0.006	–0.007	–0.013	
U*r*	0.044	0.034	0.025	0.011	0.019	0.008	0.007	0.017	
L*r*	0.041	0.033	0.024	0.013	0.021	0.008	0.008	0.015	
P(*r-rand* ≥ *r-data*)	0.001	0.001	0.001	0.001	0.057	1.000	1.000	0.638	4738

Notwithstanding the above overall findings of local spatial autocorrelation at the group level, the two dimensional local spatial analysis (2D LSA) revealed heterogeneity across the landscape (Fig. 5). In particular, a hot spot of high positive autocorrelation among groups was evident in the northeastern corner of our study, where the largest concentration of choughs was sampled. Thus, in this area of our study, neighbouring groups are genetically more similar than average: a finding that corresponds with generally low among-group genetic distances in this region.

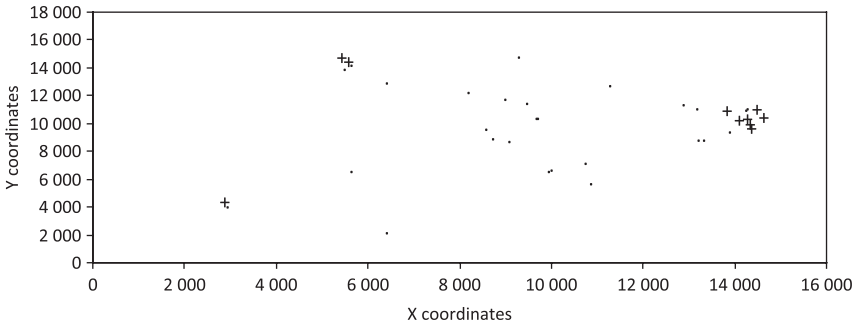

Fig. 5 Results of the two dimensional local spatial genetic analysis showing heterogeneity in genetic autocorrelation across the landscape. Crosses indicate hot spots of high positive autocorrelation among groups. Calculations were based on sampling 10 nearest neighbouring groups which represents the average number of groups found within the range of 'near neighbours' (≤ 3500 m).

Assignment index

No evidence for sex-biased dispersal was found using the assignment index. There was no significant difference between males and females in mean AIc or the variance of AIc values (males: mean AIc = 0.030 ± 0.122 SE; females: mean AIc = –0.027 ± 0.129 SE). Nor was there a difference when only adult (≥ 4 years) males and females were considered (adult males: mean AIc = –0.013 ± 0.193 SE; adult females: mean AIc = 0.012 ± 0.212 SE).

Discussion

The study population of obligately cooperatively breeding white-winged choughs showed significant genetic structure which likely reflects the interplay between social structure and dispersal behaviour. Relatedness within groups was generally high. Spatial autocorrelation analysis confirmed that groups generally consisted of close relatives, but revealed that neighbouring groups were likely to be more genetically similar than more distant groups. Positive spatial structure extended up to 4 km, despite F_{ST} estimates which showed significant differentiation among groups. Relatedness estimates, F_{ST} estimates, spatial autocorrelation analyses and assignment tests all failed to detect any evidence of a sex bias in dispersal.

Within-group structure

Estimates of mean group relatedness revealed that the majority of chough groups sampled were comprised of closely related individuals. The spatial autocorrelation analysis also exhibited strongly positive within-group genetic structure with genetic correlation estimates of a similar magnitude to the estimates of average within-group relatedness. This is not surprising given that spatial autocorrelation estimates of *r* and relatedness estimates are strongly correlated (see Banks *et al*. 2005; Double *et al*. 2005). Subadults showed stronger within-group structure than adults; however, this is not unexpected as subadults in the same group are more likely to be closely related to each other than are the adults. This finding is consistent with the obligate cooperative nature of choughs and reflects the social structure within groups.

White-winged choughs are long-lived, groups are relatively large and may be stable for more than 10 years with offspring of both sexes remaining with their natal group indefinitely (Rowley 1978; Heinsohn *et al*. 2000). In addition, the mating system is predominantly monogamous (Heinsohn *et al*. 2000; Beck 2006) and dispersal appears to be restricted by a lack of breeding opportunities (Heinsohn 1992; Beck 2006).Therefore, it is not surprising that group members are generally closely related. Similar high levels of relatedness are observed in apostlebirds, the closest relatives to choughs (Woxvold *et al*. 2006). Interestingly, the few groups which consisted of unrelated individuals were new groups whose formation had been observed during the course of the study. This is consistent with observations that new chough groups are predominantly formed when two or more unrelated 'factions' join together to form a breeding unit (Rowley 1978; Heinsohn *et al*. 2000). As a consequence, newly formed groups tend to be smaller and less closely related than established groups which generally consist of a breeding pair and their offspring from multiple years (Beck 2006).

Population structure

The study population of choughs showed significant differentiation among groups. Similar high levels of differentiation among groups have been observed in their nearest relatives the apostlebirds (Woxvold *et al*. 2006). High levels of differentiation among groups are also reported in some social mammals where polygynous mating systems and female philopatry are common and lead to high levels of relatedness within groups (Storz 1999). In such cases, differentiation among social groups is often exaggerated by group stability over long periods of time and high variance in reproductive success, where reproduction is monopolized by only a few individuals. Some of the strongest population structuring in mammals is seen in red howler monkeys (*Alouatta seniculus*) where females are philopatric and reproduction within groups is heavily skewed in favour of the dominant male who may control

a troop for over 7 years (Pope 1990). Studies of genetic structure in this species found F_{ST} values among groups between 0.142 and 0.225 (Pope 1992). In these systems, the degree of differentiation among groups is a function of the process of new group formation and the rate at which it occurs (Storz 1999). Where new groups are formed by random 'founders', a high rate of new group formation will result in lower differentiation between groups as mean relatedness in new groups will be lower than in established groups (Pope 1998). New chough groups are formed when established groups disintegrate, usually after the death of a breeder, and the resulting individuals or 'coalitions' are joined by sexually mature birds from other groups (Rowley 1965; Heinsohn *et al*. 2000; Beck 2006). The high F_{ST} estimate (0.124) among chough groups and the extremely high within-group relatedness estimates in the current study support observations from previous studies that group disintegration and the formation of new chough groups is uncommon (Rowley 1978; Heinsohn *et al*. 2000). The disintegration of established groups has only been recorded 12 times in 225 group-years of study (Rowley 1978; Heinsohn *et al*. 2000; Beck 2006).

High overall levels of differentiation among groups across the whole population can mask patterns of spatial genetic structure. Spatial autocorrelation analysis revealed exceptional genetic structure in terms of both magnitude and extent with positive structure extending well beyond nearest neighbours. Therefore, despite high F_{ST} values, neighbouring groups are likely to be more closely related than average. This is consistent with other studies of spatial genetic structure in cooperatively breeding bird species that have detected positive structure that was likely generated by philopatry and short dispersal distances, usually predominantly in males (Painter *et al*. 2000; Temple *et al*. 2006; Woxvold *et al*. 2006). Double *et al*. (2005) showed that positive spatial structure can also be generated by restricted dispersal and high levels of extra-group paternity, where males sire offspring in neighbouring territories.

In choughs, there is no evidence that extra-group paternity is common (Heinsohn *et al*. 2000; Beck 2006) and positive genetic structure in choughs probably reflects short dispersal distances and the process of new group formation. Chough groups do not defend territories, instead roaming over large, overlapping home ranges up to 1000 ha in area (Rowley 1978). Therefore, when an established group disintegrates, the potential dispersal opportunities are most obvious for nonbreeding adult birds in neighbouring groups who will encounter dispersing individuals within the area of their home range and, indeed, average dispersal distances are well within a typical home range (1300 m; Beck 2006). In addition, because newly formed chough groups tend to be smaller than established groups, new groups may be more vulnerable to intraspecific aggression (Heinsohn 1988, 1991b). For these groups, reproductive success may be improved by familiarity with the local area, or increased tolerance by neighbouring groups. Both of these are more likely if new groups are formed in the vicinity of relatives (Ekman *et al*. 2004) resulting in short dispersal distances and positive genetic structure. The predominance of short dispersal distances is supported by the results of the 2D local spatial analysis. Hotspots of positive spatial structure were observed only in those areas where multiple chough groups had been sampled within the range of 'near neighbours' (≤ 3500 m).

Sex-biased dispersal

Unlike other cooperatively breeding species where dispersal by one sex dilutes the magnitude of overall spatial genetic structure (Double *et al*. 2005; Temple *et al*. 2006), spatial autocorrelation in white-winged choughs was strengthened by a lack of sex-bias in dispersal behaviour. There was no evidence from any analysis of a sex-bias in either the tendency to remain philopatric or the distance dispersed. Estimates of relatedness (e.g. Surridge *et al*. 1999), F_{ST} estimates (e.g. Rassman *et al*. 1997; Woxvold *et al*. 2006), spatial autocorrelation analysis (e.g. Peakall *et al*. 2003; Double *et al*. 2005) and assignment tests (e.g. Favre *et al*. 1997) have all been used to detect sex-biased dispersal in other studies. Goudet *et al*. (2002) showed that many genetic tests are insensitive to a sex bias in dispersal unless the bias is extreme. However, fine-scale spatial genetic autocorrelation analysis procedures were not tested by Goudet *et al*. (2002) and emerging evidence indicates that this approach is a sensitive method for detecting sex-biased dispersal when other methods fail (e.g. Peakall *et al*. 2003; Banks *et al*. 2005; Double *et al*. 2005). Therefore, we conclude that a lack of sex-biased dispersal in choughs is real and not a consequence of a lack of statistical power. Furthermore, this genetic conclusion is consistent with observations that helpers of both sexes remain in groups over many years (Rowley 1978), and a lack of any significant difference between males and females in the frequency or distance of dispersal over a 3-year study (Beck 2006). This lack of sex-biased dispersal is unusual among birds and appears to be unique among cooperative breeders where dispersal is commonly female biased in frequency, timing or distance (Greenwood & Harvey 1982; Clarke *et al*. 1997). Even in the closest relative of choughs, the apostlebird, where both sexes are philopatric, evidence for a sex bias in dispersal has been detected (Woxvold *et al*. 2006).

While sex-biased dispersal is widespread in many philopatric species (Greenwood 1980; Clarke *et al*. 1997), the evolutionary basis of sex-biased dispersal remains a matter of much debate (Dobson 1982; Wolff 1994; Perrin & Mazalov 1999; Perrin & Goudet 2001). Perrin & Mazalov (1999) demonstrated that inbreeding avoidance could promote the evolution of sex-biased dispersal but only under a narrow

range of conditions. More often, it is considered that while inbreeding avoidance may be an important consequence of sex-biased dispersal, it has rarely been the ultimate cause (Perrin & Goudet 2001). Greenwood (1980) suggested that the direction of sex bias in dispersal was related to mating system. In avian species, female-biased dispersal is associated with a mating system in which males defend resources necessary to the acquisition of a mate or the successful production of offspring. Male philopatry is assumed to facilitate territory acquisition through local familiarity or inheritance while female dispersal is thought to be the result of inbreeding avoidance or greater flexibility of mate choice. (Although Arlt & Pärt 2008 recently demonstrated that female-biased dispersal could instead be due to sex differences in breeding site availability). In contrast, in mammal species where the mating system is predominantly polygynous, females form the nucleus of social groups to which males compete for access, adopting a mate-defence strategy rather than a resource-defence strategy, resulting in male-biased dispersal. None of these hypotheses appear to explain the unique lack of sex-biased dispersal in white-winged choughs which are not territorial and have no overt defence of resources or mates (Rowley 1978; Heinsohn 1991a). Dobson (1982) suggested that in monogamous species, competition for both mates and resources was likely to affect both sexes equally leading to equal rates of dispersal. However, this hypothesis fails to explain predominantly female-biased dispersal in many monogamous birds (Clarke *et al*. 1997). Clearly, further research into this unique exception may offer new insights into the evolution of sex-biased dispersal in birds more generally.

Conclusion

The pattern of population genetic structure that we have detected in white-winged choughs appears to reflect the combination of infrequent dispersal resulting in groups made up of close relatives and short dispersal distances which result in above-average relatedness among neighbouring groups. This structure is likely to be further reinforced by the lack of sex-biased dispersal. Natal dispersal in white-winged choughs is constrained by a long juvenile period, while dispersal by adults is constrained by a lack of breeding opportunities (Heinsohn 1992; Beck 2006). Courchamp *et al*. (1999) predict that dispersal may be a disadvantage in obligate cooperative breeders as high rates of mortality during dispersal may force groups below the critical threshold size for reproductive success. For choughs, the minimum group size for successful reproduction is three, but even larger groups can be prone to aggression and nest destruction from conspecifics (Heinsohn 1988, 1991b). The opportunities for dispersers to form breeding groups large enough to successfully fledge chicks and resist intraspecific aggression may be rare and may explain the infrequent nature of chough dispersal. When choughs do disperse, they form new groups with multiple unrelated individuals which not only results in new groups of four or more individuals, but avoids incest without a sex bias in dispersal. Although white-winged choughs are a relatively mobile species, maintaining home ranges of up to 1000 ha (Rowley 1978), they offer a unique example of a species in which social barriers to gene flow generate significant population genetic structure.

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